34—repr. Delph. Art. Ber. Staat. 10 (1892) and in Bull. Herb. Boiss. i. 335, t. 16, fig. 2 (1893). Differs fron the typical variety in having the lower part of the stem glandular-pubescent and the upper crisp-pubescent. NEBRASKA: Callaway, June 15, 1901, *J. M. Bates* in part. KANSAS: prairie, Ellis Co., June 16, 1882, *G. C. Deane;* east of Liberal, *S. D. McKelvey*, no. 2491. OKLAHOMA: near Shattuck, *R. L. Clifton*, no. 3127. COLORADO: New Windsor, June 21, 1905, *G. E. Osterhout;* Poudre Flats, north of Fort Collins, June 27, 1895, *J. H. Cowen;* along railway west of Fort Collins, June 20, 1896, *C. S. Crandall;* Denver, *I. W. Clokey*, no. 3091. TEXAS: Amarillo, *J. Reverchon*, no. 2959; Comanche Spring, New Braunfels, etc., *Lindheimer*, no. 660.

There are also two specimens collected at Noel, Missouri, by *B. F. Bush.* The lack of mature seeds in most of these specimens is a decided handicap in any effort to determine them.

D. VIMINEUM Don in Sweet, Brit. Fl. Gard. ser. 2, iv. t. 374 (1838). Texas and Mexico.

This species so closely resembles *D. virescens* in habit that I mention it here. Although it differs in the crisp-pubescent stem, occasionally somewhat bluer flowers and darker brown seeds, further collections may prove it is not more than a variety of *D. virescens.*

GRAY HERBARIUM.

NOTES ON THE DISTRIBUTION AND HYBRID ORIGIN OF × SOLIDAGO ASPERULA

RICHARD H. GOODWIN

(Plate 453)

IN 1900 Graves[1] published a note on "a little-known New England golden-rod" which Professor M. L. Fernald considered satisfactorily referable to *Solidago asperula* Desf.[2] Concerning the nature of the plant Graves wrote, "Dr. Gray, to whom most of the Massachusetts specimens were submitted, classed them doubtfully as hybrids between *S. rugosa* Mill. and *S. sempervirens* L. Later students, however, have been more inclined to regard this form as entitled to specific rank." Since then, accumulating evidence from field observations has led botanists to agree with Dr. Gray. The seventh edition of Gray's Manual (1908) lists the plant as a probable hybrid between *S. rugosa* and *S. semperivrens.*

[1] RHODORA **2** (15): 57–59. 1900.
[2] Desfontaines, Cat. Hort. Paris ed. 3: 403. 1829.

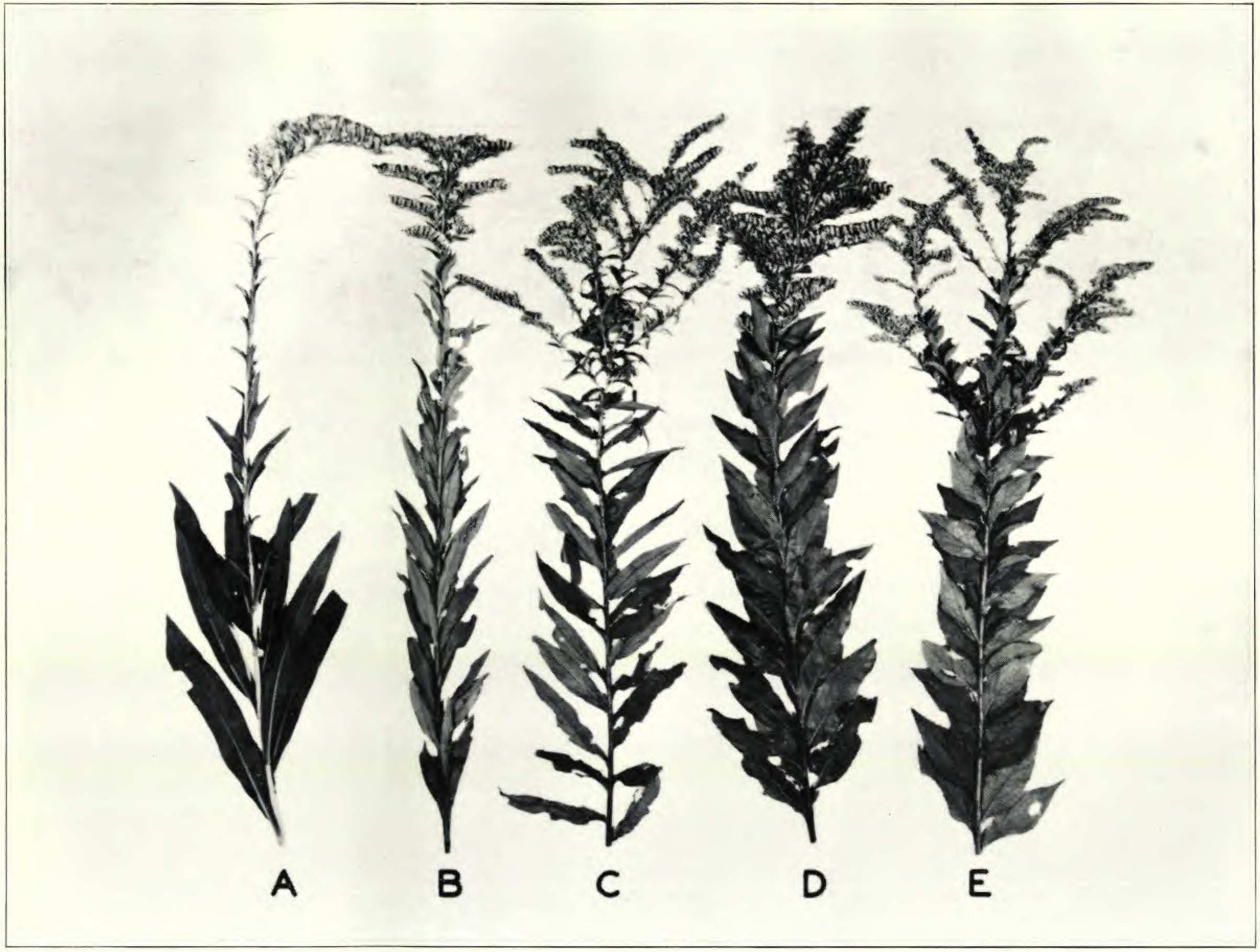

Fig. A, Solidago sempervirens. Figs. B, C and D, × S. asperula, showing intergradations between A and E. Fig. E, S. rugosa. All specimens from the reclaimed saltmarsh on the Charles River, Cambridge, Massachusetts, September 19, 1932.

In connection with the hybrid origin of × *S. asperula* Desf., the geographical distribution of this plant and of its two alleged parents is of interest. FIGURES 1, 2 and 3 show the northeastern distributions of *S. rugosa, S. sempervirens* and × *S. asperula* respectively.[1] Knowlton, Weatherby, and Ripley[2] listed *S. rugosa* as generally distributed and *S. sempervirens* and × *S. asperula* as maritime species. Inspection of the maps shows that the range of × *S. asperula* does not extend

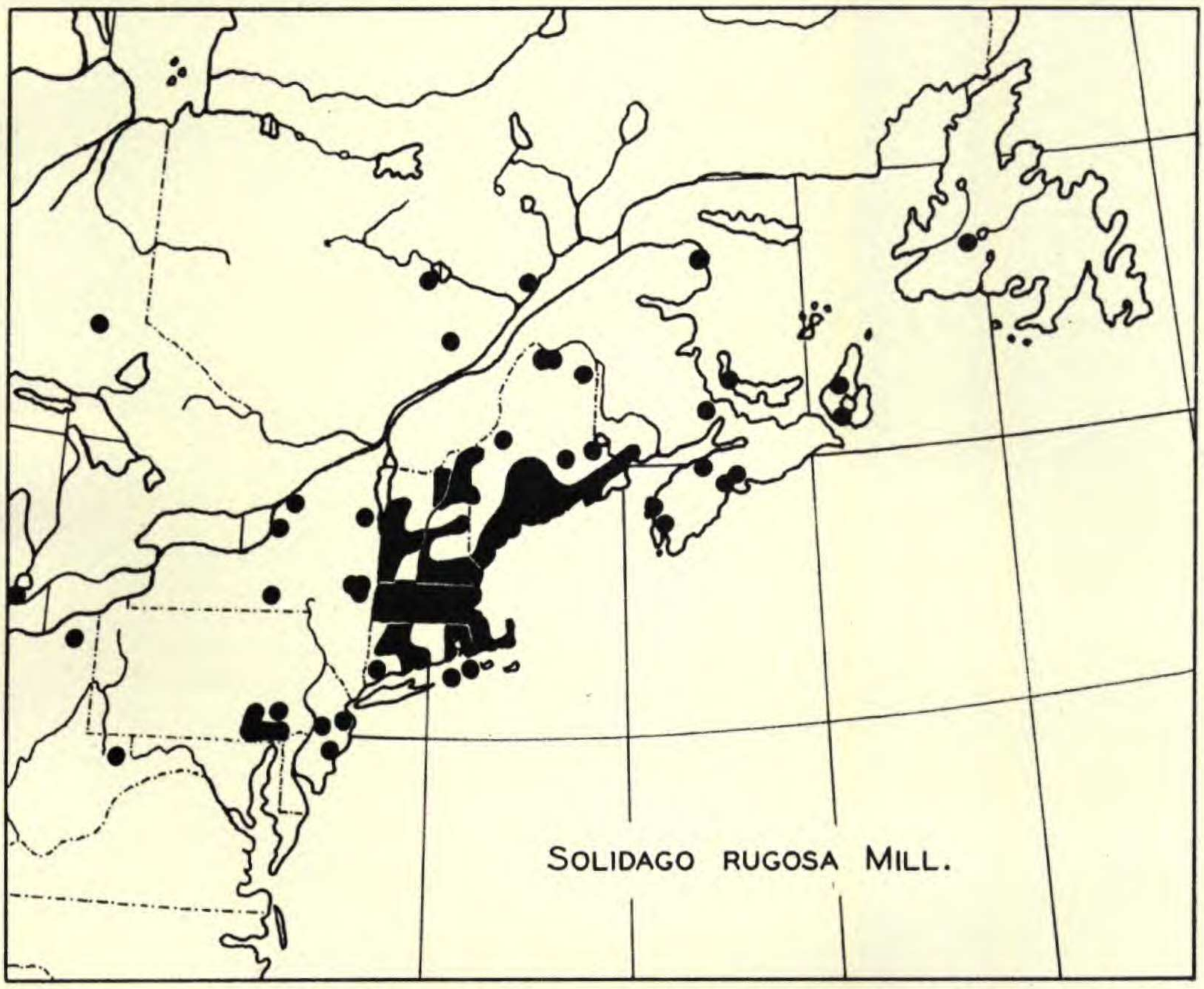

FIG. 1. Northeastern Occurrence of SOLIDAGO RUGOSA.

beyond that common to the two supposed parents. Notes on a large number of the more recent collections of × *S. asperula*, moreover, specifically mention the close proximity of both *S. rugosa* and *S. sempervirens*.

× *S. asperula* may be found most readily along the margins of salt-marshes adjacent to unmowed open land where *S. sempervirens* and *S. rugosa* are both flowering in abundance. Ideal conditions for

[1] Further collecting would undoubtedly extend the distribution of these plants as now shown on the maps. Specimens from the localities indicated may be found in the collections of the Gray Herbarium, of the New England Botanical Club, of Dr. R. H. Wetmore, or of the author.

[2] RHODORA 27 (316): 56–65. 1925.

natural hybridization between *S. rugosa* and *S. sempervirens* were indirectly brought about in Cambridge, Massachusetts, by the closure of the dam at the mouth of the Charles River estuary in 1908. The subsequent ecological changes which took place in the flora of the salt-marsh between the Cambridge cemetery and the Charles River have been described by Mr. Walter Deane.[1,2] By 1912 considerable salt had been leached from the marsh.[1] Although most of the salt-

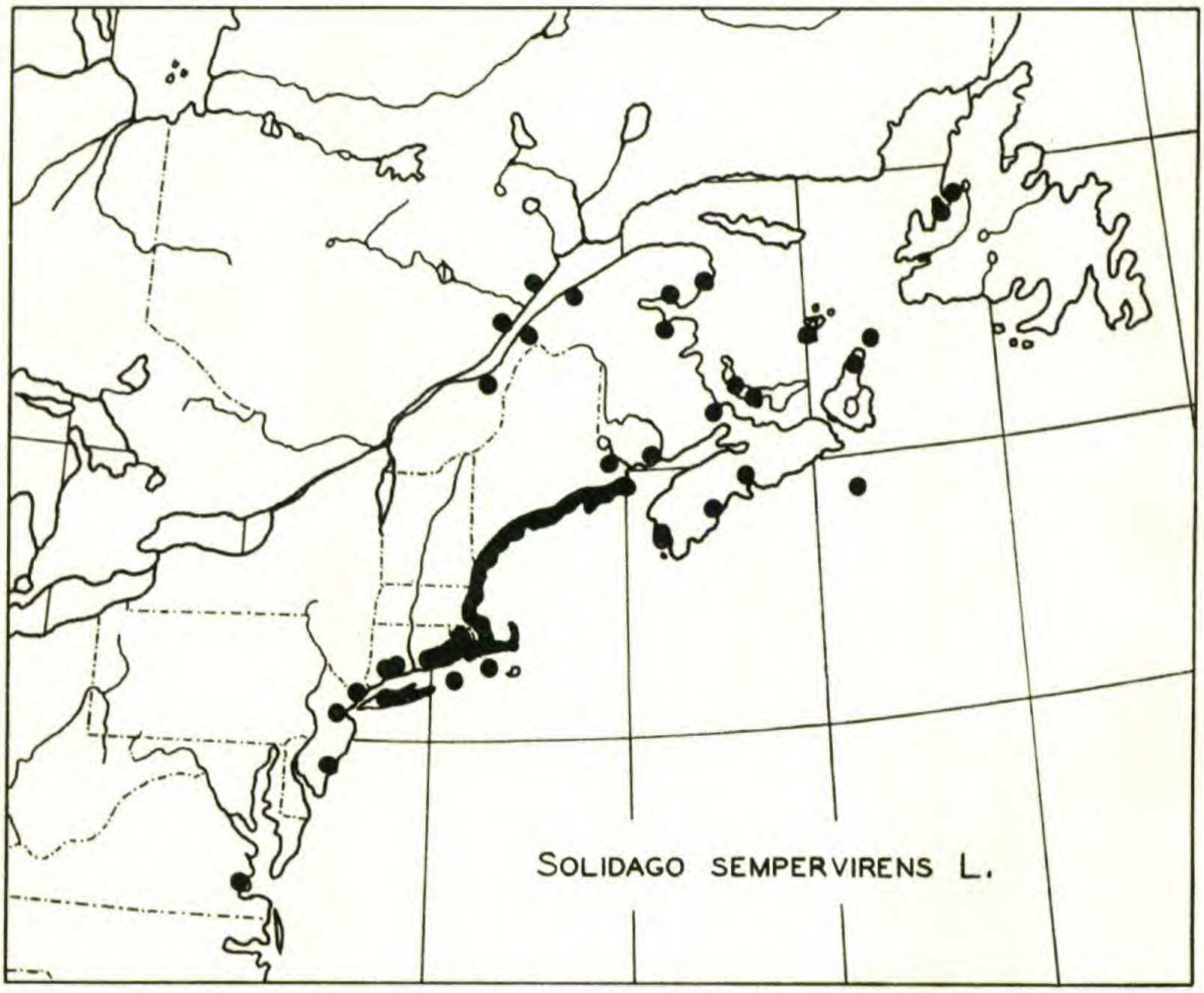

FIG. 2. Northeastern Occurrence of SOLIDAGO SEMPERVIRENS.

marsh plants, including large stands of *S. sempervirens*, were still present, a host of weeds and fresh-water plants had already invaded the area. Among these was *S. rugosa*. In 1923 *S. sempervirens* was one of four maritime plants which Mr. Deane mentions as still persisting. Mr. Deane did not record × *S. asperula* in his original list nor in his supplement published in 1926. A number of specimens of this plant were collected from the area in 1923, however, by Dr. R. H. Wetmore, and it seems probable that it was growing there at an even earlier date. FIGURE 4 shows the distribution of *S. rugosa*, *S. semper-*

[1] RHODORA **17** (203): 205–222. 1915.
[2] RHODORA **28** (327): 37–40. 1926.

virens, and × *S. asperula* over this area in the fall of 1933. *S. rugosa* was common throughout; *S. sempervirens* was restricted to scattered patches; while × *S. asperula* was abundant, but most frequently associated with *S. sempervirens*. Furthermore, × *S. asperula* showed a tremendous variability, exhibiting many intergradations between *S. rugosa* and *S. sempervirens*, as shown in PLATE 453.

The foregoing evidence coupled with the many morphological

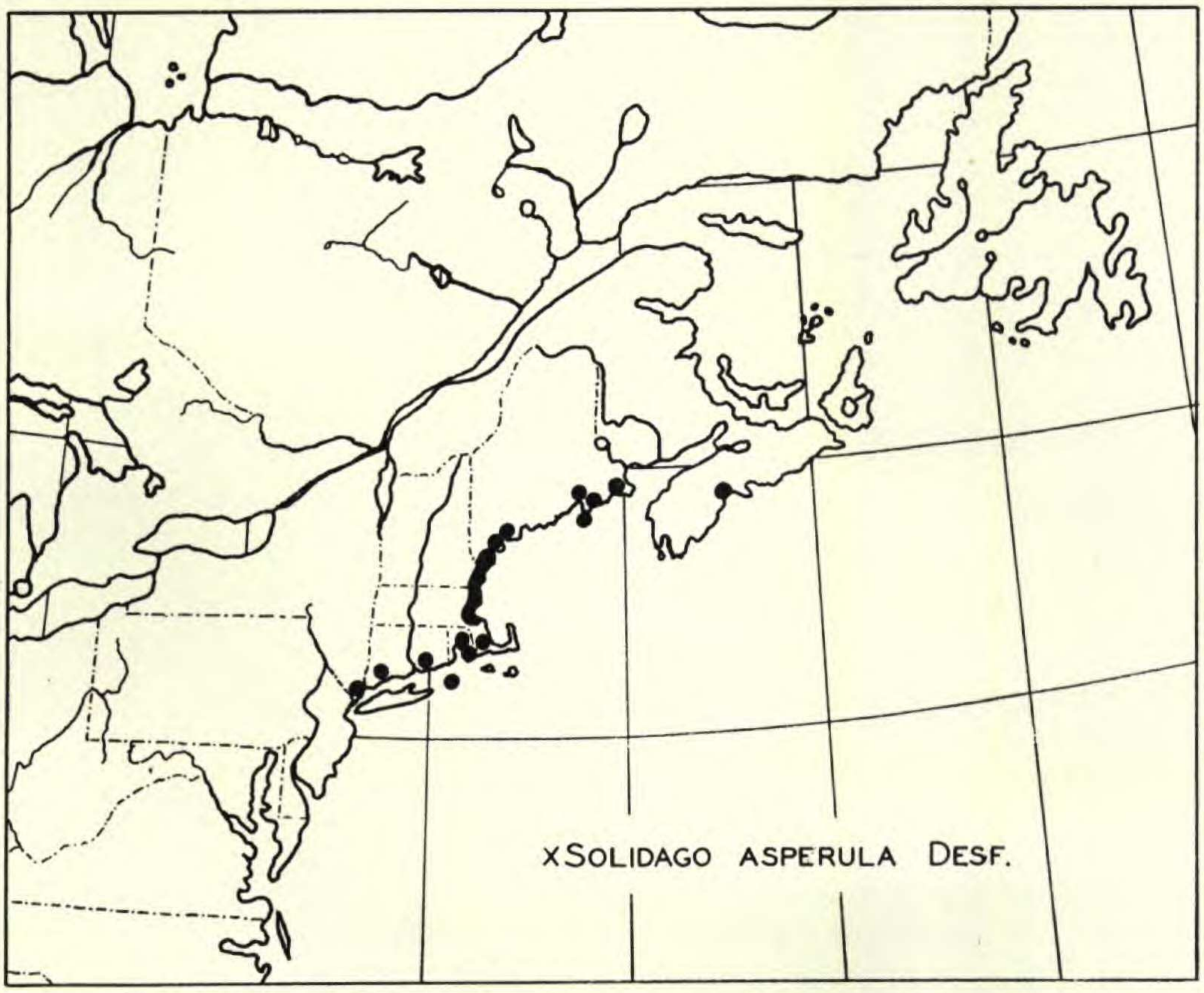

FIG. 3. Northeastern Occurrence of × SOLIDAGO ASPERULA.

characters intermediate between *S. rugosa* and *S. sempervirens* points to the hybrid origin of × *S. asperula*. The fact that these plants set abundant seed indicates that they are fertile and that second generation hybrids and back-crosses with the parents may occur.[1] This would account for the variability encountered in nature.

Genetical work carried out by the writer during the past five years has proved the validity of these conclusions. *S. rugosa* and *S. semper-*

[1] Since hybrid plants are usually sporadic in occurrence and have always been found growing close to their parents, back-crosses between hybrids and their parents should be far more frequent than second generation hybrids.

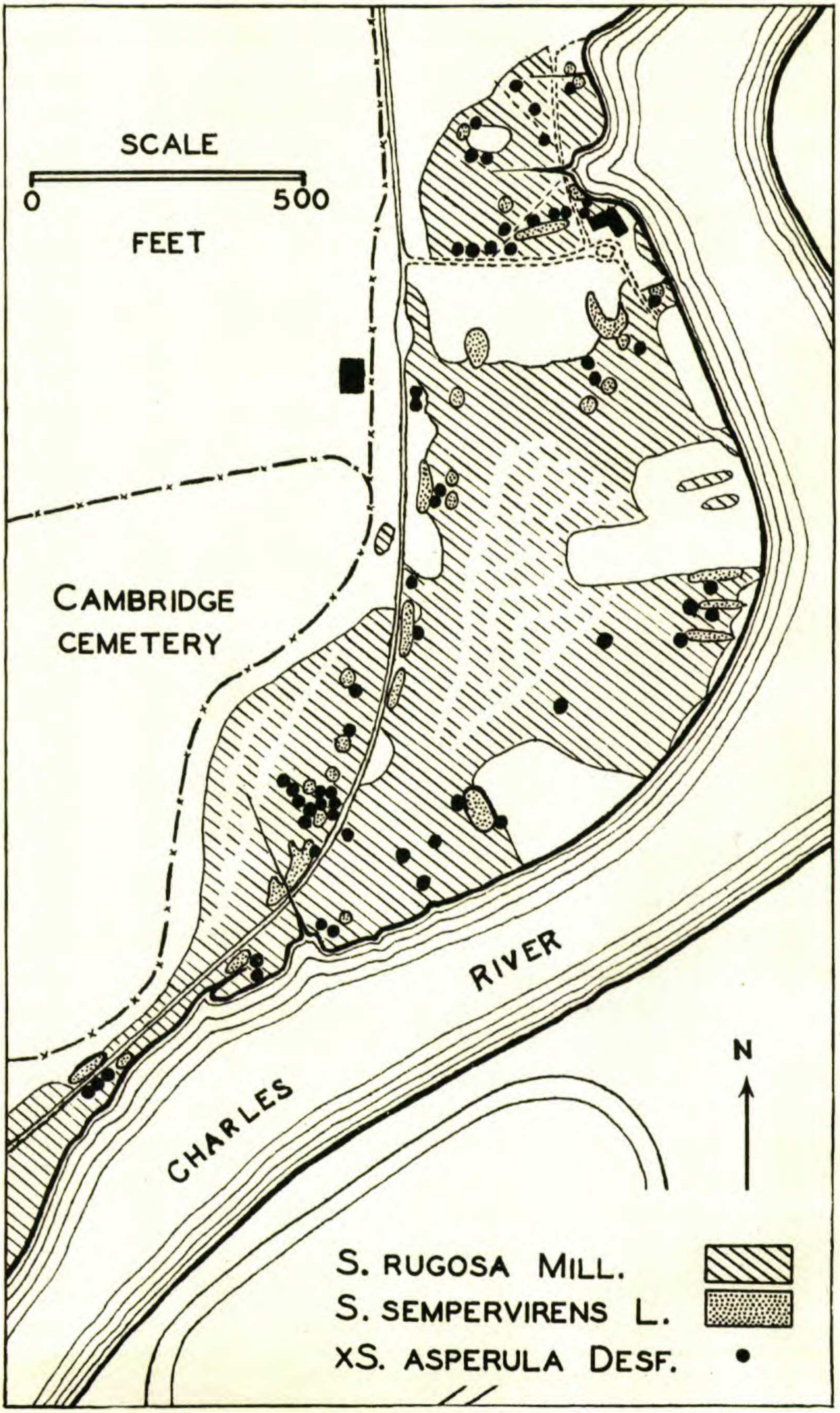

FIG. 4. Occurrence near Cambridge Cemetery of SOLIDAGO RUGOSA, S. SEMPERVIRENS and × S. ASPERULA.

virens[1] were used as stock material during the investigation. Pollinations were carried out in the greenhouse under carefully controlled conditions. The technique will be described in a subsequent paper. The results obtained were as follows:

1) F_1 hybrids were obtained from reciprocal crosses between *S. rugosa* and *S. sempervirens*. Their morphological and floral characters were intermediate between the parents and identical with those of typical plants of × *S. asperula*.[2]

2) Pollination experiments with these hybrids have proved them to be inter-fertile and self-sterile like their parents. A second generation has been brought to flower. Plants of the F_2 generation showed a complete range of intergradations between the two parental types.

3) Back-crosses were obtained between F_1 hybrids and both parents. These varied in appearance between the F_1 hybrid and the parent with which it was back-crossed.

This genetical evidence proves conclusively that × *S. asperula* is a hybrid between *S. rugosa* and *S. sempervirens*. Further, the variability of the second generation hybrids and back-crosses offers an explanation for the variability of × *S. asperula* in nature. The plants growing in an area such as the reclaimed salt-marsh on the Charles River display a complex of variable forms which might well confuse anyone who had not bred and grown these hybrids and back-crosses from seed.

Although *S. sempervirens* and × *S. asperula* are restricted to a maritime distribution, they have been grown from seed in the greenhouse and garden in light loamy soil just as successfully as has *S. rugosa*. Hence it would seem to be factors other than salinity which limit their distribution. The distribution of × *S. asperula* may not be confined to the immediate vicinity of salt water by ecological factors, as is generally the case with its maritime parent. Any spread of the hybrid inland, however, would result in these plants back-crossing exclusively with *S. rugosa*. In this way the characters of *S. sempervirens* would soon be swamped out.

[1] The original plants of *S. sempervirens* were obtained from pure stands on the sand dunes at Ipswich, Mass., while those of *S. rugosa* were collected on a high hill in Belmont, Mass.

[2] The description of × *S. asperula* Desf. in Gray's Manual, 7th edition, is adequate for genetical material grown by the writer in the greenhouse, except that the lowest cauline leaves of my specimens may reach a length of 3.6 dm. Graves' measurements are also correct except for these leaves. In nature the lowest cauline leaves have usually withered at the time of flowering and are frequently not present in herbarium material. Furthermore, there is a tendency for these plants to grow larger under greenhouse conditions.